

arrivals and stayed longer. However, they later lost their attachment to the feeding station, resulting in a shorter stay there. It seems likely that this in turn causes a decline in the social hierarchy.

Summary

Cygnus cygnus cygnus were observed at close range during artificial feeding at Lake Hyoko. Individual swans were recognized by bill pattern, and family groups by already identified individuals. Trends in hierarchy among family groups could thus be recorded; reversals in dominance were, however, often noted.

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SOCIAL BEHAVIOUR OF WINTERING *CYGNUS COLUMBIANUS* *BEWICKII*

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Introduction

Among birds, continued association between parents and their fledged offspring is most typical of co-operatively breeding species, where offspring remain on their natal territory or in a group home range throughout the year (eg Zahavi 1976). However, such relationships also occur in some species that do not breed co-operatively, among waterfowl *Dendrocygnini*, *Anserinae* and some *Tadornini* (Kear 1970).

In many co-operative breeders, the advantages of extended parent–offspring relationships may lie in the assistance by older offspring in caring for younger offspring. This may increase the inclusive fitness of both parents and offspring: in several species the productivity of groups with ‘helpers’ is higher than that of a pair alone. In cases where this has not been demonstrated, it has been suggested that ‘helpers’ provide valuable assistance in defence of the group territory.

With the exception of the seabirds which continue to feed their young during the first winter, the advantages of extended parent—offspring relationships in birds that do not breed co-operatively are not obvious, since these species do not usually defend a territory all year nor do the parents continue to feed or brood the young. It has been suggested that in migratory swans and geese, parents are guiding their young to traditional wintering areas (Ogilvie in Scott *et al* 1972). However, this does not explain why migratory ducks do not maintain family bonds nor why parents and offspring continue to associate after fledging in some sedentary species (eg *Cygnus olor*, *Cygnus atratus*). It has also been suggested that parents are protecting their offspring from predation by keeping watch while the offspring feed (Owen 1972) but this again fails to account for species differences in parent—offspring relationships. Another suggestion, that parents may be protecting their offspring from feeding competition, has arisen from the work of Boyd (1953) and Raveling (1970) who showed that goslings were less successful in aggressive encounters when separated from their parents.

The present paper reviews the results of a detailed study of the behaviour of wintering *Cygnus columbianus bewickii* in the UK (D Scott 1978a), in which the advantages and disadvantages to different individuals of maintaining close proximity to family members were investigated, to determine whether protection from feeding competition was important. The pair bond was also examined to discover if there were any similar advantages to mates of maintaining proximity.

First, however, it was necessary to investigate whether success in competition affected access to food, subsequent survival or reproductive success. Although individual differences in competitive ability or dominance have been demonstrated in flocking birds, eg *Tadorna tadorna* (Patterson 1977), few studies have investigated the relationship between age or presence of associates on dominance or the effect of dominance on access to resources or survival. However, a number of studies have concluded, following Lack (1954), that access to food in winter may be important in regulating population density in birds.

A good opportunity to investigate competition and the advantages of being a member of a group or unit is provided by *C. c. bewickii*. Individuals vary in the pattern of black and yellow on the bill and can be recognized without the necessity for marking (P Scott 1966). Families (mated pairs with their cygnets), pairs without offspring, and single individuals are easily visible as units within winter flocks. Age differences are apparent up to 2½ years and the sexes are distinguishable with 89% accuracy (D Scott 1978a). Finally, a large proportion of individuals return to the same wintering grounds in successive years, including the Welney Wildfowl Refuge, Norfolk, and the Wildfowl Trust, Slimbridge, where there is access for observation at close range (Evans 1978; D Scott 1978a).

Study site

The study was carried out between 1974 and 1976 at the Welney Wildfowl Refuge,

Norfolk, on the Ouse Washes, where 200 to 300 swans regularly came for the grain provided at 0930, 1530 and sometimes 1900 hours. Over 1000 were sometimes present during cold weather. Observations were made both from the main hide on the Refuge and on surrounding fenland where the birds often fed during the middle of the day on agricultural crops (winter wheat, sugar beet and waste potatoes). Fen flocks also contained many individuals that were unfamiliar with the grain provided in front of the hide, spending the whole day feeding on crops. Some additional observations were made on flooded meadows in the vicinity (at Swavesey and Earith) where small flocks stayed for short periods.

Observations were made from October when the first swans arrived through to March or April when the last swans left on migration for the Soviet Arctic. Additional observations were made at the Wildfowl Trust, Slimbridge in Gloucestershire, where *C. c. bewickii* has been studied in detail since 1964 (Evans 1978, 1979). Data collected at Slimbridge on weights were also used.

Methods

Methods of recognizing individuals by differences in bill pattern and of recording and filing patterns have been described in detail elsewhere (Rees 1981). In the study described here, 583 different individuals were identified and all regular visitors to the lagoon in front of the hide (200 to 300 individuals) could be identified instantly from memory (see Bateson 1977).

Individuals were also classified according to age, sex, size and paired status. While adult swans are completely white, cygnets (first winter birds) can be distinguished by their grey plumage. Second winter birds can be identified by traces of grey feathering on the head and neck. Beyond this it is not possible to age unknown birds. However, in this study, third winter birds could be identified as those which had been present the previous winter as second winter birds.

Sex was estimated from size, since adult males are 13% heavier than females (Evans and Kear 1978). Evidence from 150 birds at Slimbridge sexed by estimation of size and subsequently caught and sexed cloacally showed that sex had been estimated with 89% accuracy. For paired birds ($n = 100$) the accuracy was somewhat higher (95%) than for single individuals ($n = 50$, 78%). The sex of cygnets was probably estimated with lower accuracy, since male cygnets average only 10% heavier than females (Evans and Kear 1978). Of 14 cygnets at Slimbridge whose sex was confirmed cloacally, ten had been correctly sexed by estimation. In this study, nine of the 19 cygnets studied in detail have returned in subsequent years and their sexes confirmed in relation to temporary or permanent mates.

The three main units within the flock, families, pairs and single individuals, were rapidly apparent. White birds associating with pairs were, in all but one case, offspring of previous years associating with their parents. While being obvious on

account of the resemblance of parents and offspring, which has now been demonstrated statistically (Bateson *et al* 1980), this has been confirmed at Slimbridge where birds ringed as cygnets have been observed at the ages of two, three and four (and occasionally older) associating with their parents (Evans 1978).

Individuals were also classified as large, medium or small. The accuracy of size estimates was checked by examining the weights of birds caught at Slimbridge whose size had been estimated previously.

Data were collected in three ways:

- (a) Systematic observations of particular 'focal' individuals were made during the hour-long periods in which birds loafed in front of the hide awaiting feeds. It was necessary to sample each bird for a short time in a rota, in order to obtain data on different individuals in similar situations. In the sampling rota five individuals were watched, each for one minute every ten minutes. In each hour-long session, focal individuals were of one class (ie all male parents, all female parents, etc) and the class was rotated. Most focal individuals were observed in at least five sessions (ie usually 25 minutes) throughout the winter.

During each sample minute, all signals and interactions were recorded, as well as the identity of the interactant and whether associated birds were present. At the end of each minute, point samples of the following were taken: distance to mate, cygnets or parents, distance and identity of three unrelated nearest neighbours and general activity (feeding, alert, preening, sleeping). Distances were recorded in swan lengths (sl): 1 swan length = 0.67 m.

- (b) Flock scan samples of one hour were made after the morning feed from 1030 to 1130 in front of the hide and on the fens on alternate days. During these samples, all instances of aggressive encounters involving display were recorded, including details of their duration and intensity, and the identities of all participants.
- (c) In front of the hide, data were also collected on an *ad lib* basis. Aggressive encounters involving display and their outcomes were recorded whenever possible in order to investigate dominance.

Three measures of individual differences in competitive ability or dominance were used: (a) who beat whom; (b) proportion of different opponents (individuals or units) beaten of all encountered; (c) proportion of encounters won. (This measure was considered less satisfactory than (a) and (b) because some individuals and units scored extreme values after interacting with the same opponents several times; it was used only where data were otherwise scanty).

Results are given in detail (with statistics) elsewhere (see D Scott 1978a, 1980a

and 1980b), as are details of the analyses involved.

Results

Partners of pairs and family members were together in 90% to 95% of aggressive encounters. For this reason, the dominance relationships of units (families, pairs and single individuals) are considered first. Differences in dominance of individuals within units are investigated afterwards.

Dominance relationships between units within the flock

Both in 1974/75 and 1975/76 it was possible to rank units according to who beat whom so that the top-ranking ones differed greatly in success from the bottom-ranking ones. However, it was not possible to arrange units in a strictly linear hierarchy since circular relationships (ie relationship going up the hierarchy) occurred, but at most in 10% of cases.

Despite circularities, dominance relationships were relatively constant throughout the winter. The mean percentage of a unit's relationships which changed (usually once but very occasionally twice) during a winter was only 4.6 in 1974/75 and 7.1 in 1975/76.

Between years, dominance relationships were again remarkably constant. 81.8% of the dominance relationships of six units were in the same direction in both 1974/75 and 1975/76.

Dominance relationships were also stable in different situations. Observations of known individuals on the fens showed that their success in encounters when feeding on crops was closely related to the proportion of opponents they beat in front of the hide.

Dominance relationships between classes within the flock

The most obvious differences in competitive ability within the flock were between different kinds of unit. As in geese (Boyd 1953; Raveling 1970), families generally dominated pairs without offspring, which dominated single individuals. Thus, in front of the hide at Welney and at Slimbridge, the proportion of encounters in which families beat pairs and pairs beat singles was higher than vice versa. However, in contrast to geese, there was no significant tendency for large families to dominate smaller ones. Furthermore, there were many exceptions to the rule that parents beat pairs which beat singles.

In front of the hide, it became apparent that 'anomalous' relationships in which a particular pair dominated a particular family, or a single individual dominated a pair, could be stable throughout the winter. In 1974/75, two of 14 'anomalous'

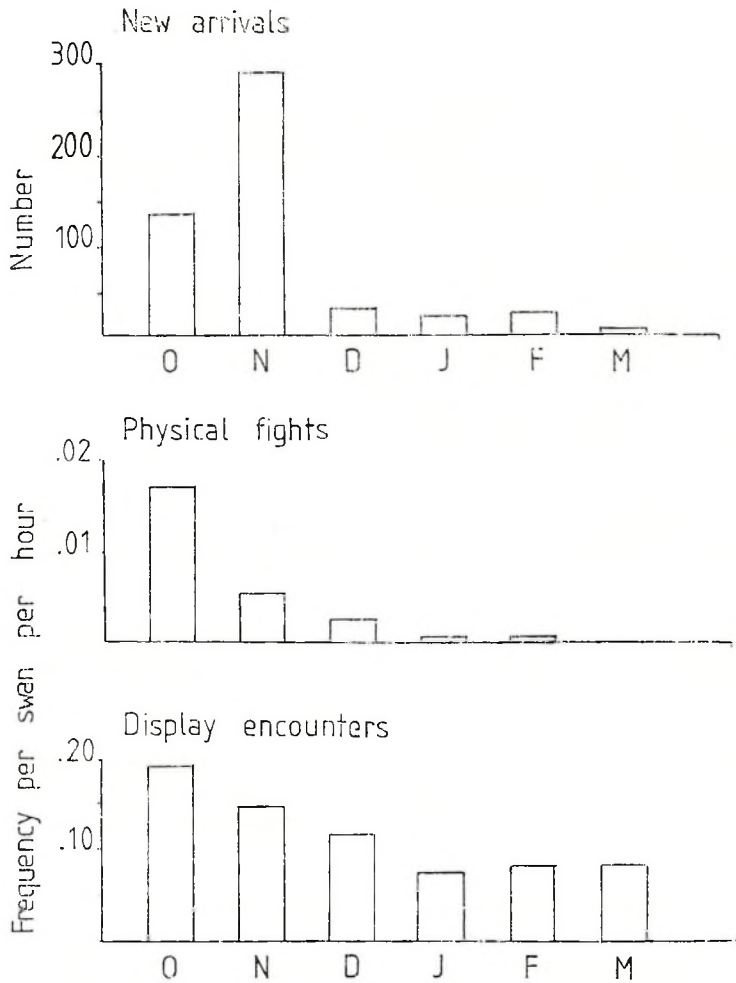


Fig 1. Decline over the winter in the number of newly arrived birds, physical fights and aggressive encounters involving display.

relationships where pairs dominated parents changed during the winter and in 1975/76, 12 of 28 such relationships changed.

Establishment of dominance relationships

When most birds arrived, in October and November, frequencies of display encounters and physical fights were high and subsequently declined during the winter

(Fig 1), except for a small peak in February, corresponding to a small influx of swans apparently passing through on northward migration. It seems likely that the early high frequency is associated with new arrivals for two reasons. First, on landing, 75% of units became involved in aggressive encounters within the first five minutes. Second, units were observed in more encounters on their first day than on subsequent days.

That these encounters on arrival were associated with establishing dominance relationships is also suggested by the following evidence: firstly, the outcomes of encounters with particular opponents on the first day remained the same on subsequent days but they became less intense; secondly, units were involved in display encounters more often with particular opponents on their first day as well as with a greater total number of opponents than on later days.

Units appeared to establish relationships with many birds within the first day. One newly arrived pair with three cygnets interacted with a total of 40 different opponents within 2½ hours. For this family, the number of encounters in each half hour, their duration and intensity all decreased over this period, as did the duration and intensity of encounters with nine opponents encountered more than once.

Maintenance of dominance relationships

The reduced frequency of encounters raises the question of whether individuals are able to recognize each other. Among the swans, there are two observations which are difficult to explain if individuals did not recognize at least some other birds within the flock. First, individuals returning after short absences did not show higher frequencies of encounter than on other days and showed lower frequencies than on their first day in the season (Table 1). Secondly, individuals of similar rank

Table 1. Mean number of encounters on different days.

On first day	6.18 ± 3.4	n = 22 individuals
On return day after absences of any length (mean length was 16 days, n = 75 absences)	0.72 ± 0.47	n = 36 returns
On return day after absences of <10 days	0.46 ± 0.78	n = 13 returns
On return day after absences of >10 days	0.87 ± 0.58	n = 23 returns
On all days except first	0.69 ± 0.15	n = 14 individuals

and similar paired or family status (with equal numbers of cygnets if present) should be less likely to be able to deduce each other's relative dominance from overall physical appearance than individuals dissimilar in these respects. However, individuals were sometimes observed avoiding similar opponents (established as dominant in a previous encounter) without any provocation.

Variables related to dominance

Size, weight and sex were all related to dominance. Large birds tended to dominate a higher proportion of opponents than small birds when the effects of age, sex, paired status and immediate context (presence/absence of associates) were taken into account. There were positive correlations between size and rank for five classes of birds. At Slimbridge 28 of 37 encounters were won by the heavier opponent. Males tended to be more dominant than females according to the proportion of opponents beaten during focal samples. It seems likely that the lower dominance of females is associated with their smaller size and lower weight than males.

Since winners tended to be heavier, it might be expected that age up to 2½ years (when adult weight is probably reached) might be associated with dominance, but there was little evidence that this was so.

Units arriving in October tended to be more dominant than those arriving in November or later. Dominant units also spent more days in the area than subordinate ones and spent a greater proportion of days between arrival and departure in front of the hide. However, it was not possible to determine whether it was the most dominant individuals in each class that arrived first or whether the individuals that arrived first became most dominant.

Observations on the fens indicated that dominant individuals spent more time feeding than subordinates. In addition, differences in dominance were correlated with differences in breeding success the following summer (as measured by the number of cygnets accompanying their parents in the subsequent winter). Moreover, birds that brought cygnets one year but not the next were lower in rank than average for parents in the year before they failed to bring cygnets.

Effects of proximity of associates

The competitive ability of most unit members appeared to decrease when they were separated from the remainder of the unit. On flooded meadows, cygnets won 75% of aggressive encounters when less than four swan lengths from their parents and only 33% of encounters when farther away. In front of the hide, six cygnets observed consistently during the winter 1975/76 dominated a smaller proportion of different opponents when away from their parents than when with them. In addition, offspring of previous years, associating with their parents, were less dominant when away from their parents than in the presence of their parents (Fig 2). Moreover, those arriving earlier in the season than their parents became more dominant once their parents had arrived. There were no apparent differences in effect of proximity of offspring to male or female parent.

Partners of pairs also suffered reduced competitive ability when separated. In front of the observatory, the success in encounters of focal female paired birds without

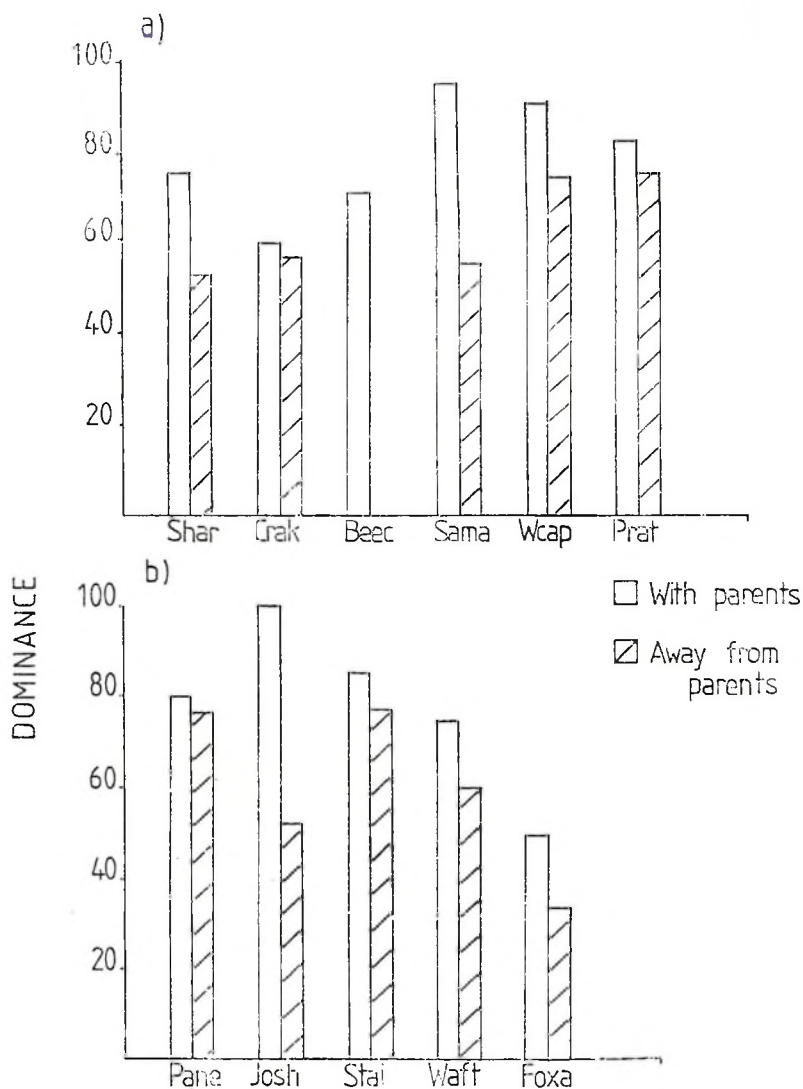


Fig 2. Dominance of second (a) and third (b) winter offspring with (< 4 sl) and away (> 4 sl) from parents.

cygnets showed a significant negative correlation with distance from mate (Fig 3), and the same was true for focal male paired birds. However, there was no evidence that parents suffered decreased ability in the absence of their cygnets.

Female paired birds

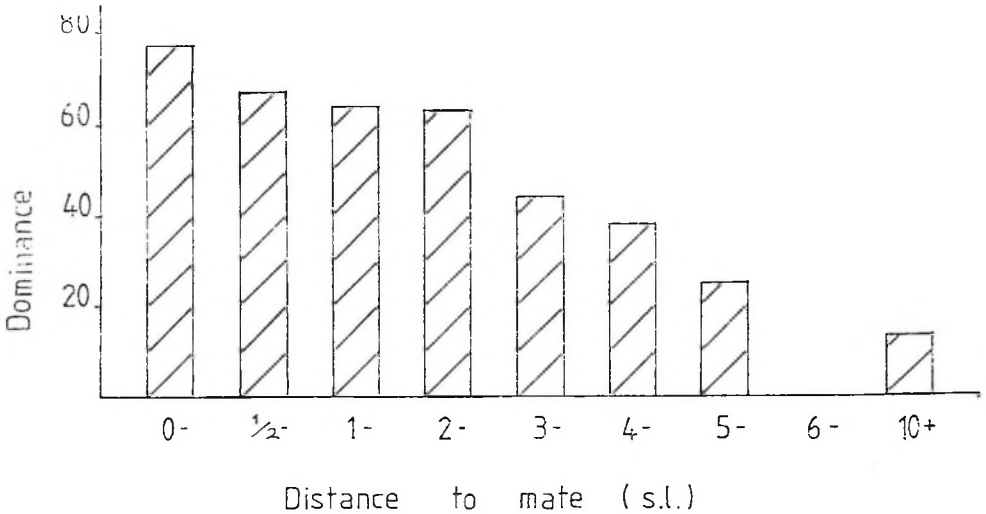


Fig 3. Relationship between dominance and distance to mate for female paired birds.

Proximity to other unit members was also related to the amount of time individuals spent feeding. On flooded meadows, cygnets spent only 52.1% of the time feeding when away from their parents (>4 sl) and 81.5% when close to them, and there was a significant negative correlation between time spent feeding and distance to parents. Female paired birds on the fens spent only 61.4% of the time feeding when away from their mates (>4 sl) and 80% when with them, again a significant difference. For male paired birds on the fens, this tendency was still apparent: they spent 56% of time feeding when away and 75% when with their mates, but the difference was not quite significant.

Assistance in aggressive encounters

Parents frequently intervened in encounters on behalf of their cygnets when the latter were being threatened by other birds. Such interventions occurred in 34% of all cygnet encounters with others on flooded meadows. The presence of the parents appeared to inhibit other individuals from threatening cygnets. All six focal cygnets were threatened by others more often when away from their parents than when with them. In addition, subordinate individuals usually moved out of the way of family units, often without any visible signs of aggression from the latter. As a result of this inhibitory effect, cygnets in their parents' presence essentially assumed their parents' rank.

In similar ways, partners of pairs assisted each other in encounters. 'Supported' encounters comprised 25.8% of those in which female paired birds were involved and 22.5% of those in which male paired birds were involved. The influence of an inhibitory effect was also apparent in the increased frequency with which partners were threatened when away from their mates. This was more marked for female than for male paired birds: females were threatened four times more often when away from their mates, while males were threatened only twice as often.

Both partners of pairs and members of family units were particularly close to each other during the display encounters which always preceded fights. It is possible that the assistance of the female in these displays (and perhaps the presence of cygnets) reinforced the displays of the male.

However, since dominance relationships depended ultimately on ability to win physical combat, and, since females almost never joined in such fights, it is not clear why the presence of the female enhanced the competitive ability of the male, unless he was more willing to fight when his mate was present than when she was absent.

Variation in proximity

Unit members should maintain greater proximity in dense flocks than in dispersed flocks. In addition, members should be closer when feeding on foods over which competitive interactions are frequent than where interactions are infrequent. Since interactions among swans were more frequent during feeding in front of the hide than on the fens, and on waste potato crops than on winter wheat, unit members should be closer in the former of each of these comparisons than in the latter. Finally, since competitive ability was related to body size, weight and sex, small individuals and females should maintain greater proximity to family members than large individuals or males. These predictions were largely upheld.

There were two results which failed to support the predictions. During the feed in front of the hide, when density was exceptionally high, partners of pairs, and family members were separated for most of the time and reunited afterwards. Partners of pairs also maintained greater distances to each other relative to the distances to other flock neighbours when feeding on waste potatoes than on winter wheat.

Proximity of unit members also varied in a number of other ways. Among families, proximity decreased with the age of the offspring: parent—cygnet proximity decreased over the winter and relationships between parents and previous years' offspring were usually loose. Average distances between third winter offspring and parents were greater than between second winter offspring and parents. In contrast to the peaceful relationship between cygnets and parents, the latter frequently threatened their offspring in later years.

Parent—cygnet proximity was greater among subordinate families than among dominant families. Despite this relationship, the cygnets of dominant parents tended to be more successful in encounters both alone and with their parents than those of subordinate parents.

In contrast to the greater proximity of members of subordinate families, partners of pairs in which the male by himself was high-ranking tended to maintain greater proximity than those where the male was low-ranking. Pairs in which both partners were either very large or very small tended to spend less time together than other pairs.

Proximity of partners was also greater when they had no accompanying offspring than when offspring were present. But since the offspring frequently positioned themselves between their parents, this is an unsurprising result. All unit members maintained greater proximity during roosting than during feeding.

Discussion

The advantages to individuals of maintaining proximity to other unit members were apparent in terms of increased competitive ability and time spent feeding by most individuals in the presence of family members compared with when separated from them. The evidence indicated that differences in competitive ability were important in affecting access to food and subsequent breeding success and that individuals differed in ability according to size, weight and sex. In accordance with this variation in dominance, female cygnets (ie small cygnets) tended to maintain greater proximity to their parents than male cygnets and, as adults, female paired birds benefited more from the proximity of their mates. Correspondingly, cygnets benefited more than their parents from maintaining proximity. In addition, parent—offspring proximity declined as offspring grew older and approached adult size. But since second winter birds are still significantly lighter than adults and third winter birds may also be below adult weight, these birds may continue to gain substantial protection by associating with their parents.

If competition for food occurs in other waterfowl species, these findings may provide an explanation for species differences in the extent of parental care in waterfowl. While evidence suggests that cygnets and goslings do not reach adult weight until they are more than one year old (Owen *et al* 1977; Evans and Kear 1978), immature ducks appear to reach adult weight in their first autumn (Owen and Cook 1977). If competitive ability is determined by relative body size in ducks, first winter individuals may not require parental protection in competition with conspecifics. The difference is essentially a function of body size, since large birds have slower growth rates (Ricklefs 1973) and therefore take longer to reach adult size. This argument is supported by the fact that prolonged parental care occurs in other large, slow-growing waterfowl (eg *Tadornini*) which form flocks in the non-breeding season.

There may be many other benefits associated with parental care, including guiding offspring to traditional wintering grounds or particular feeding sites, or protecting them from predation. However, by themselves these benefits do not account for the differences in parental care between waterfowl species.

The results also provide a possible explanation for the early formation of pair bonds in many duck species. If competition for food is significant and if males are able to protect females (Ashcroft 1976) or partners gain mutual assistance in aggressive encounters, early formation of pair bonds may be advantageous.

In *C. c. bewickii* the evidence also indicated that benefits of proximity could sometimes be counteracted by costs, with the result that unit members separated. This was apparent during the feed in front of the hide, when density was exceptionally high and unit members usually became separated. In this situation it seems likely that the costs of maintaining contact in the confusion of birds jostling for food outweighed any benefits of proximity. Costs of proximity may help to explain why unit members were closer during roosting than during feeding as in *Anser brachyrhynchus* (Lazarus and Inglis 1978) if competition occurs within as well as between units. Such costs could also account for the tendency of mates to be farther apart when feeding on potatoes, where competitive interactions were frequent, than on wheat, where they were infrequent. However, this raises the question of why parents and cygnets should be closer on potatoes than on wheat, unless parents spend more time protecting the cygnets than feeding themselves. This may indeed be the case, since parents spent less time feeding than did pairs without cygnets, especially during the first part of the winter.

Costs of proximity in terms of feeding interference between unit members may also explain variation in proximity of mates and family members in other species and in different situations. Evidence suggests that in some goose species and in some situations, mates and family members are usually each other's nearest neighbours while, in others, they may be at greater distances with other birds between them.

In *C. c. bewickii* the advantages of proximity were particularly great for the offspring of dominant families and females mated to dominant males. The first of these findings parallels the results of a number of studies of primate species, where offspring 'inherit' their mother's rank, giving the offspring of dominant mothers priority of access to resources. As yet it is not known whether the effect continues into adult life among swans as it does among primates. However, there is preliminary evidence that the cygnets of dominant families remained dominant among yearlings in the following winter, even when they were completely alone, ie before their parents had arrived. Long-term consequences of early differences between individuals are being discovered increasingly in other species and further study may reveal their extent in *C. c. bewickii*.

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Summary

Winter flocks of *Cygnus columbianus bewickii* comprise well-defined units: mated pairs with accompanying offspring, unaccompanied pairs and single individuals. Pairs and families feed, preen and sleep together, and are particularly close during aggressive interactions between units, especially those involving conspicuous display. This paper reviews the findings of a detailed study in UK which investigated the possibility that assistance in competition for food is an important advantage of staying close together.

Individuals differed substantially in competitive ability; in the presence of other unit members, most individuals were more dominant and spent more time feeding than when separated from them. Large, heavy birds and males tended to be more dominant, while small lighter birds and females suffered greater decreases in competitive ability when separated from other unit members. Since dominant individuals and units showed a tendency to spend more time feeding and to breed more successfully (as measured by the number of young returning the following winter) than subordinates, the advantages of assistance in competition may be considerable.

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SEASONAL VARIATION, SEX DIFFERENCES AND HABITU- ATION OF TERRITORIAL BEHAVIOUR IN *CYGNUS OLOR*

J DEMAREST

Introduction

Among Old World immigrants resident around Long Island Sound, none is more striking than *Cygnus olor*. In spring, sometimes upwards of 50 birds gather on the bays, inlets and estuaries. Some will leave their flock to find a pond or secluded cove to breed. Others may disperse to find an area uninhabited by mated swans. In the past few decades, however, this swan has undergone a population explosion and uninhabited areas have become uncommon. As a consequence *C. olor* has